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Behavior and movements of Indian meal moths (*Plodia interpunctella* Hübner) during commodity infestation ☆

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Abstract

A model warehouse with carefully regulated environmental conditions was used to study the behavior of adult Indian meal moths during commodity infestation. Sequences of moth distributions in the warehouse, calculated by spatial analysis, clearly showed the coordinated movements of moth populations from eclosion to death. Many facets of adult behavior in a warehouse were coordinated with the photoperiod. Adult moths emerged at the end of a photophase and fairly rapidly moved to the walls and, to a lesser extent, to the undersides of the commodity pallets. Most females are mated in the first 24 h after emergence, largely during the scotophase. Air circulation within the warehouse probably compromised pheromone-directed guidance of males to females, although pheromones may still have a major role in regulating other aspects of male mating behavior. When mating subsided, many of the males flew upwind to the air circulating unit, but only during the photophases. The females moved to the return air side of the warehouse and then migrated towards the same end as the males, but only during the scotophases. They moved from pallet to pallet largely by walking on the warehouse floor and laid eggs in or on the cups of commodity. Direct oviposition on the commodity during the infestation period was lower than expected, probably because commodity odors were dissipated by air circulation and did not provide appropriate orientation. At 144 h after emergence, 90% of the moth population had died. Published by Elsevier Science Ltd.

Keywords: Egg laying; Indian meal moth; Mating behavior; Moth behavior; Moth distribution; Moth movement; *Plodia interpunctella*; Spatial analysis

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1. Introduction

The process of commodity infestation by stored-product insects can conveniently be divided for purposes of study into three stages: movement to the commodity, establishment in the commodity, and population growth. Knowledge of the behavioral patterns that bring pest species successfully through each stage of this process would be of considerable value in preventing damage and contamination of food products. Several studies have dealt with the behavioral elements that lead to infestation. Willis and Roth (1950), for example, studied the attraction of the red flour beetle, *Tribolium castaneum* (Herbst), to flour and found that the degree of attraction is determined, at least in part, by the moisture content of the flour and the nutritional state of the insect. Hagstrum (1973) and Hagstrum and Leach (1973) described movement of adult *T. castaneum* into flour and the resulting distributions of eggs and adults. LeCato (1978) described infestation of various spices in closed spice cans by the cigarette beetle *Lasioderma serricorne* (F.).

Arbogast and Mullen (1978) studied the distribution of eggs laid by the Indian meal moth, *Plodia interpunctella* (Hübner), among discrete food resources and discussed the oviposition behavior inferred by changes in spatial pattern with increasing numbers of females. However, little information was provided on the behavior and movements of the moths during commodity infestation. Conventional observational techniques and analyses obtained by periodic counts of moths resting on various warehouse surfaces and plotting the numbers versus time for each surface, provides useful information on the emergence and mortality of moths along with identifying the warehouse sites moths occupy during an infestation. These observations can be complemented by spatial analysis, which accurately depicts movement of the moth population within the warehouse.

The study reported here examines the behavior of male and female moths during the infestation of a commodity stored at defined environmental conditions in a model warehouse. Commodity infestation begins when moths first appear in the warehouse and ends when they oviposit either on or near the commodity. During this period there is considerable movement of moths within the warehouse as they seek suitable resting surfaces for expanding and hardening their wings; as they seek out partners for mating; and, as they seek suitable sites for oviposition. These movements of moths can be portrayed as a series of contour maps, each of which is a snapshot of adult spatial distribution, sequenced in time. Collectively, these sequential distributions of moths taken throughout the infestation period provided a moving pattern that reflected the moth population movements in the warehouse. Conventional observations provided an interpretation of the physiological bases underlying these movements of the moth population.

2. Materials and methods

2.1. Test facilities

All tests were conducted in two model warehouses (Fig. 1), $9.1\,\mathrm{m} \times 3.7\,\mathrm{m} \times 2.4\,\mathrm{m}$ high, that were maintained at $30^\circ \pm 0.7^\circ\mathrm{C}$ with baseboard heaters and an air conditioner controlled by a commercial electronic heat/cool thermostat. Each warehouse was of frame construction with an outer corrugated metal covering, 8.9 cm thick extruded styrofoam insulation placed between the

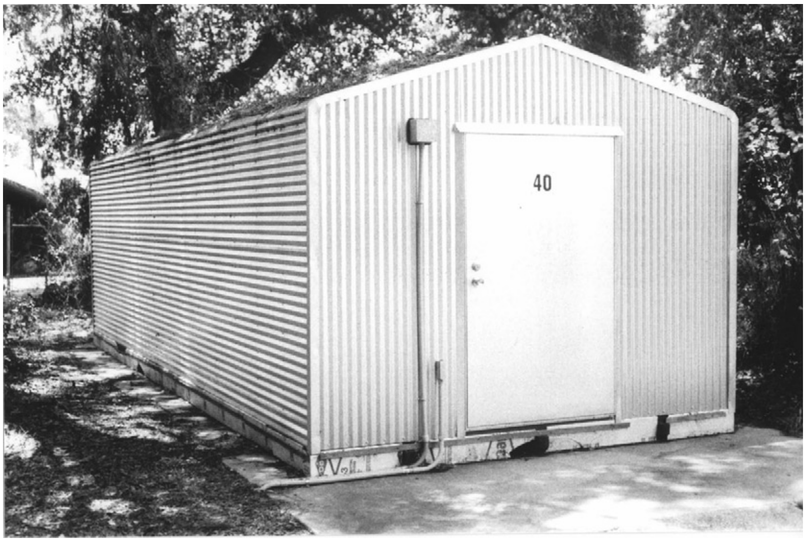

Fig. 1. Model warehouse used for studying the behavior and movements of synchronized populations of Indian meal moths during commodity infestation using carefully regulated environmental conditions.

studs and the rafters and covered inside with 1.3 cm sheet rock painted with a washable, off-white enamel. The air conditioner fan ran continuously, circulating air within the warehouse in a circular fashion as indicated (Fig. 2) with no introduction of fresh air. In these experiments, the ambient relative humidity measured on the pallets supporting the commodity cups was $60 \pm 10\%$. Lighting in each warehouse was provided by six, 40 W, cool white fluorescent bulbs and was regulated to provide a 16 L:8 D photoperiod that was synchronized with the photoperiod used in the laboratory for rearing standardized test insects. Indigenous moth populations were prevented from occurring in the warehouse by removing any accumulated debris immediately after a test. Prior to the introduction of test insects for a new test, the warehouse was inspected to ensure that it was clean and free of non-test insects.

2.2. *Test insects*

Indian meal moths were reared at 30°C, 70% r.h. in plastic boxes (14 cm $\times$ 19 cm $\times$ 9 cm deep) on the standardized *Plodia* diet described by Silhacek and Miller (1972), consisting of ground dog food, rolled oats, cornmeal, whole wheat flour, wheat germ, brewer's yeast, glycerol, and honey. A 16 L:8 D photoperiod was maintained except that the scotophase was routinely initiated at 12:00 p.m. The newly emerged moths used in these experiments were obtained by placing several tightly wound corrugated cardboard rolls, 1 cm high $\times$ 10 cm in diameter, on the diet surface in standard rearing boxes for 24 h during the wandering stage. Larvae crawled into the rolls during this 24-h period to spin cocoons and pupate. The rolls, containing larvae and pupae, were placed in a rearing incubator for an additional 6 d after which the 6- to 7-day-old pupae was transferred to the warehouse.

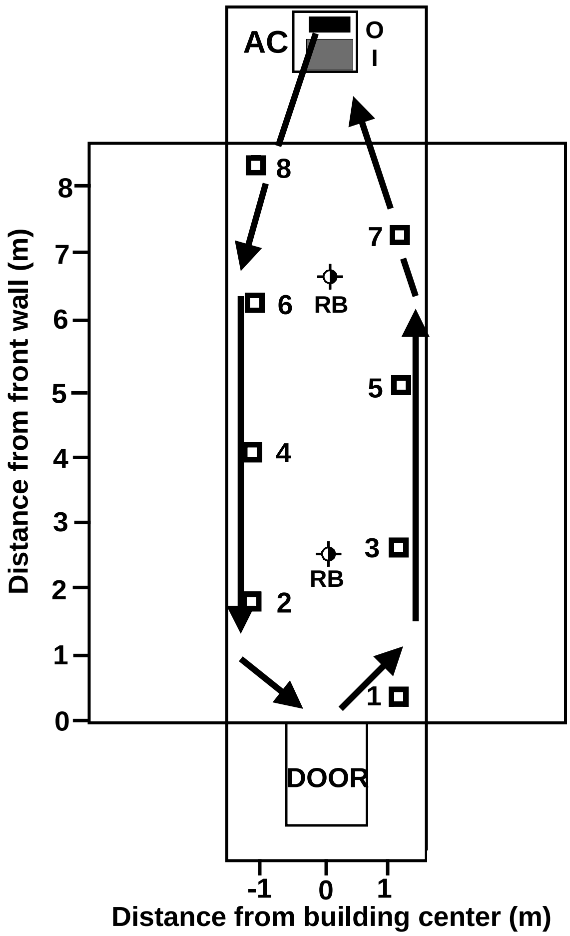

Fig. 2. Diagrammatic representation of the model warehouse showing the air circulation pattern within the warehouse. The air circulating/cooling unit (AC) circulated air within the warehouse, continuously entering at an average velocity of 551 m/min through the air outlet (O) of the unit and entering the AC through the return air inlet (I). Also shown are the positions of the two release boxes (RB) that contained pupae for moth emergence and the eight numbered pallets that supported the commodity cups.

2.3. Experimental

Shortly before initiating a test, open paper cups (9.5 cm diameter × 8.9 cm deep) of *Plodia* diet were placed in the warehouse on each of eight plywood pallets (30.5 cm × 30.5 cm × 1.25 cm). The pallets rested on four clear plastic vials that elevated them about 10 cm above the warehouse floor (Fig. 3). In the experiments reported here, four commodity cups were placed on a pallet and each cup contained 50 g of *Plodia* diet.

The test was initiated 2 h before the first scotophase by suspending two release boxes (RB, Fig. 3), each contained about 800, 7-d ± 0.5-d-old pupae into the warehouse at two release points located 1.5 m above the floor at approximately 3 m from each end. The moths were allowed to emerge in the warehouse over a 48-h period, after which time the release boxes were removed.

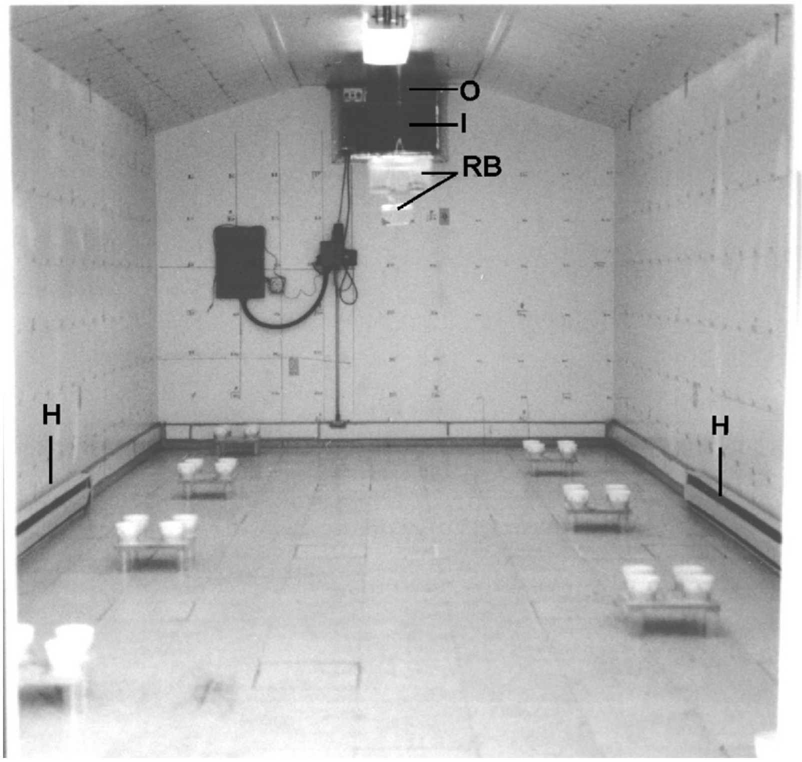

Fig. 3. Interior of model warehouse during a typical experiment showing open cups of commodity on elevated plywood pallets and the suspended moth release boxes (RB). The baseboard heaters (H) and the air circulating and cooling unit with the air inlet (I) and outlet (O) are shown. Heating and cooling were thermostatically controlled at 30°C and a 16 L:8 D photoperiod was provided by three pairs of 40 W fluorescent bulbs arrayed down the center of the ceiling.

2.4. Sampling

The distribution of the moth population in the warehouse was assessed by counting the moths located on a predetermined sampling grid (Fig. 4) of squares (30.5 cm/side) marked on the walls and floor of the warehouse. The numbers of moths on the sample squares were counted every 4 h throughout the 108 h test period except the count at the midpoint of each photophase was omitted. In addition, moths on the commodity, the cups, the pallets (topside and underside), including the supporting vials and the floor space directly under the pallets were counted at the same times as the wall and floor counts and this count was collectively designated the pallet count. The air inlet filter (black plastic foam, 30.5 cm × 91.5 cm) on the air circulating and conditioning unit (Fig. 3) was also monitored for resting moths.

A measure of the number of eggs laid directly on the commodity was estimated by counting the number of offspring that developed in two of the commodity cups which were capped and removed from the warehouse at 56 h. At 30°C, eggs hatch 62 h after oviposition (Silhacek and Miller, 1972); therefore, the number of larvae counted in these cups 13 d after being capped at 56 h and incubated at 30°C could only arise from eggs laid directly into the cups. When the two

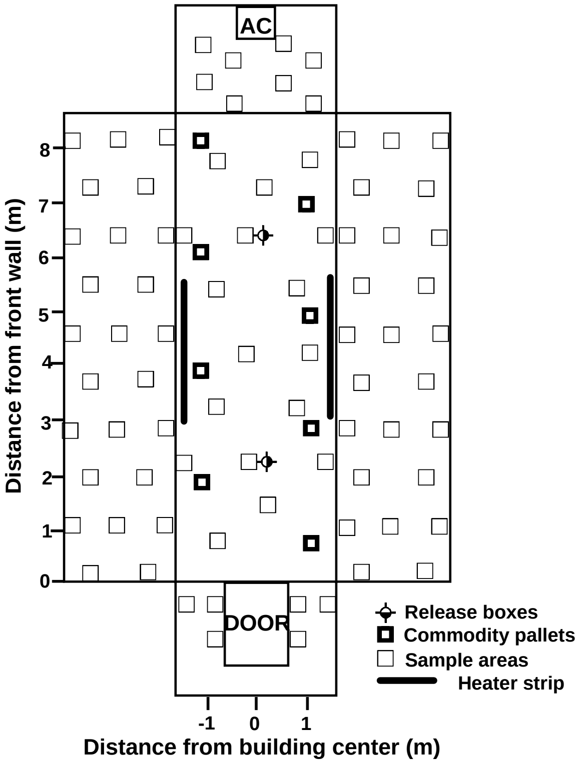

Fig. 4. Diagrammatic representation of the model warehouse showing the test grid pattern with the counted grids identified.

commodity cups were removed at 56 h, they were replaced with fresh cups of commodity which were subsequently capped and removed at 108 h for incubation and counting as described before. The two remaining cups placed on the pallet at the outset of the test were capped and removed at 168 h for incubation and counting. The 108 and 168 h counts consisted of larvae originating not only from direct oviposition inside the cup, but also crawl-in larvae arising from eggs laid outside the cup.

2.5. Analyses

The number of moths occupying the walls and floor in the warehouse was estimated by counting the number of moths on the preselected grid squares laid out on the four walls and floor (Fig. 4). The total numbers of moths occupying the walls and the floor was obtained by extrapolating from the counted grid areas to the total surface area. The ceiling was not included because it afforded a resting area for only an occasional moth; usually this occurred near the end of the test and then only in the vicinity of the air conditioner. In addition, the number of moths associated with the pallets and the return air filter were obtained by direct count of the moths. The total numbers of moths found in each of these four areas were determined five times each day throughout the 4.5 d infestation period. With conventional analysis, the total number of moths

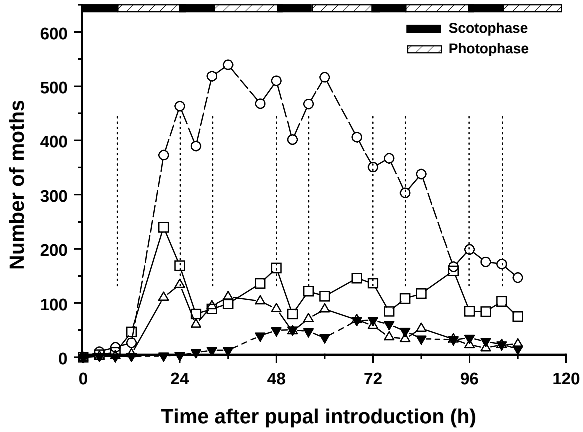

Fig. 5. Distributions of moths in the model warehouse on the four resting surfaces monitored at intervals during the infestation period. This graph is the average of four replications analyzed by the conventional method. The standard errors for each point in the graph are summarized in the appendix. The dotted lines represent the points of transition between light and dark.

counted or estimated for each of the four warehouse areas was plotted against time. The average of four tests are shown in Fig. 5.

A more revealing analysis of moth population localizations and movements in the warehouse was obtained by analyzing the same data using spatial analysis (Surfer 7.0, Golden Software, Golden, CO). Spatial analysis depicted the moth distributions in the warehouse at each sampling time during the infestation period. The x–y coordinates of the grid squares and the corresponding numbers of moths found on each square were entered in Surfer for contour analysis (Keckler, 1995; Arbogast et al., 2001). The software placed the observed moth numbers at the appropriate coordinates on a floor plan of the warehouse, which had been entered as the base map. Surfer then created a denser grid of moth densities by interpolation using one of several algorithms as described by Arbogast et al. (2001). A sequential comparison of the density plots provides the pattern of movement followed by the moth population during the infestation process.

3. Results and discussion

3.1. Moth emergence

The emergence of moths in the warehouse was closely synchronized with the photoperiod. Eighty $\pm$ 10% of the moths emerged during the 12-h period preceding the second scotophase (Fig. 5), the remainder emerged during the 12-h period preceding the third scotophase. The synchronized emergence of Indian meal moths as a result of entrainment by photoperiod has been previously reported by Lum (1974a, b).

Shortly after emerging in the open release boxes (RB, Fig. 3), many of the moths dropped to the floor and rapidly moved to resting areas on the walls or the undersides of the commodity pallets.

Usually the moths walked or ran to these resting areas, but some, whose wings had already expanded and hardened, did fly.

3.2. Moth mating

The females began their calling behavior within a short time after reaching a suitable resting area, releasing pheromone (Lum and Brady, 1973) that elicited a flutter response in the males. This usually occurred on the warehouse walls, but some calling females were observed on the undersides of the commodity pallets and the sides of the two release boxes as well.

We postulated that distinct concentration gradients of pheromone for male moth orientation do not form in a closed warehouse containing a high level of pheromone that is mixed by an air circulation system. The initial moth density of 400 calling females in our $73\,m^3$ warehouse would provide the high level of pheromone and an air inlet velocity of 551 m/min, moving $27.5\,m^3$ of air/min should provide sufficient circulation (Fig. 2) to disrupt discrete plume formation needed for effective male orientation.

3.3. Male behavior

In such a closed warehouse where there is little likelihood of pheromone plume formation, the flutter dance behavior of the males may provide an alternative strategy for males to seek out females for mating. This male "fluttering" has been previously reported by Brady and Smithwick (1968) and by Lum (1974a, b). Mating occurred when a fluttering male made physical contact with a calling female. A sampling of moths in the warehouse on day 3 revealed that all of the females had mated, even though an occasional calling female was still observed. In such an environment the pheromone concentration may still act as a switch that turns on the mating behavior, even though it is limited in providing the directional guidance of a classical pheromone plume response.

We observed also, that males begin to gather on the inlet filter of the air-circulating unit on the second and third day after emergence (Fig. 3). At this time, the pheromone levels in the warehouse would have been reduced because most females had mated (Lum and Brady, 1973) and only a few were still calling. We speculate that at reduced pheromone levels and still no distinct pheromone plume, the mating response is still turned on, but, instead of the flutter dance, the males respond by flying upwind anticipating a female encounter somewhere upstream. As they approach the fan unit, the males probably tire and drop down out of the oncoming air stream, coming to rest on the air inlet filter directly beneath the air outlet.

3.4. Female behavior and egg laying

The mated females remained closely associated with the commodity pallets for most of their lives. They moved from pallet to pallet during the scotophases, congregating first on the pallets along the return air side of the warehouse before progressing towards pallet 7 (Fig. 2). At 104 h the females (and a few males) were largely centered on and around pallet 7. Random sampling of at least 10 female moths at intervals throughout the infestation period revealed that all had mated

Table 1
The number of Indian meal moths resulting from direct infestation of diet in commodity cups. Cups were capped at 56 h, removed from the warehouse and incubated for an additional 13 d in the rearing incubator before counting the number of developing larvae

Pallet no.	No. larvae ± SD
1	78.0 ± 31.9
2	43.0 ± 22.4
3	62.5 ± 20.5
4	127.0 ± 43.3
5	99.5 ± 55.1
6	168.0 ± 31.8
7	181.0 ± 22.0
8	132.5 ± 28.9

and contained either a full or partial complement of eggs; only rarely did we observe a living female that was devoid of eggs.

Although the female moths were closely associated with the commodity pallets for most of their lives, direct oviposition on the commodity was modest, as indicated by the number of developing larvae in cups removed at 56 h after moth emergence (Table 1). Exposing the commodity for 168 h, which not only extended the time for direct oviposition, but also permitted infestation by crawl-in larvae, increased the number of infesting larvae by 50%. However, the number of larvae infesting the fresh commodity (108 h) cups that replaced the 56 h cups were found to contain 2.5 times as many infesting larvae as the 56 h cups. These observations indicated that females might be hampered when seeking a suitable oviposition site by the circulating air in the warehouse impairing their orientation to the commodity cups. This impairment could result from disruption of commodity odor concentration gradients or by dissipating odor emissions from the commodity.

Shaaya et al. (1991) reported that oviposition by Indian meal moth females was initiated by juvenile hormone secretion which occurred when they mated. Factors, such as food odors and moisture, may then provide additional cues that guide the females to the commodity and further stimulate oviposition.

3.5. *Moth distribution, conventional analysis*

The localization of moths in the warehouse space was visualized by sequentially sampling the moth distribution at 4-h intervals during the infestation period. Some newly emerged moths remained on the release boxes for various periods of time and were not included in the counts. Others quickly dropped from the release boxes, in many cases even before their wings had expanded and hurried across the floor to either a wall or a pallet to a suitable resting site. The estimated numbers of moths located on the floor, the walls, the commodity pallets, and the return air grill of the air conditioner were plotted against time (Fig. 5). Comparing the estimated numbers of moths on the various surfaces indicated that the majority of moths sought out the

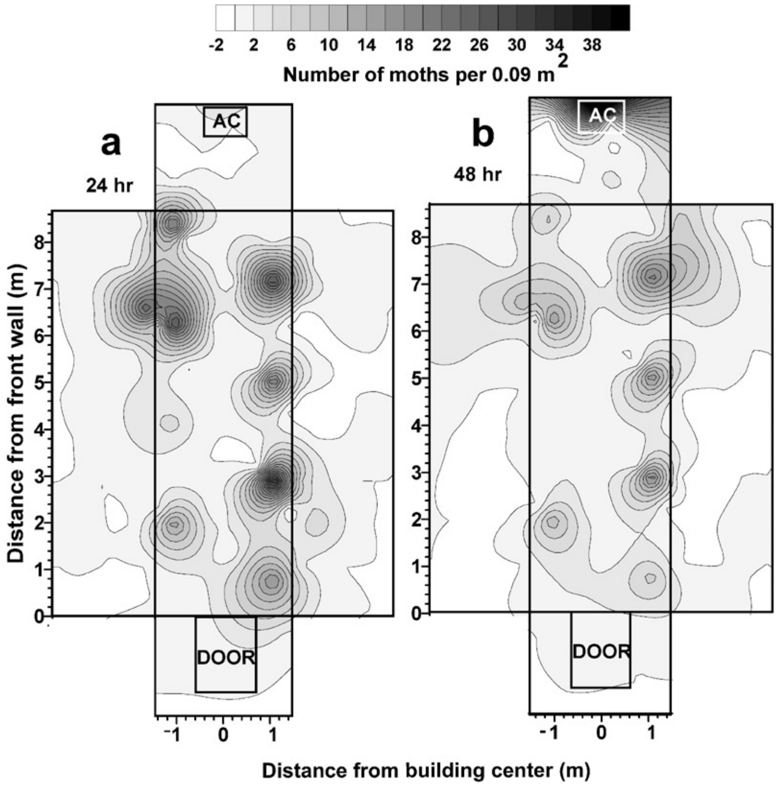

Fig. 6. Distributions of moths in the warehouse as revealed by spatial analysis at (a) 24 h; (b) 48 h; (c) 72 h; and (d) 108 h after initiating the experiment by introducing $6\frac{1}{2}$-d-old pupae into the warehouse space at 0 h. Additional analyses (not shown) taken at 4-h intervals throughout the 108 h test period provided a more detailed depiction of the moth movements in the warehouse during the infestation period. The data shown here represents only one set of the replicates presented in Fig. 5, but is typical of all four replicates.

walls as their initial resting site following their emergence just prior to the second scotophase. Fewer moths were associated with the commodity pallets and the floors. This distribution of moths remained relatively static throughout the infestation period with the exception that the moth population on the wall declined over time with a concurrent assembly of males on the return air filter of the air conditioner as previously noted.

3.6. Moth distribution, spatial analysis

Spatial analysis provided a much more detailed picture of population localization and movement in the warehouse. Comparison of sequential moth distributions during the infestation period revealed that the moths were responding to several factors in the warehouse environment. At 24 h (Fig. 6a) the distribution of moths in the warehouse indicated that the moths moved from the emergence boxes to the nearest suitable resting areas such as the walls and the commodity

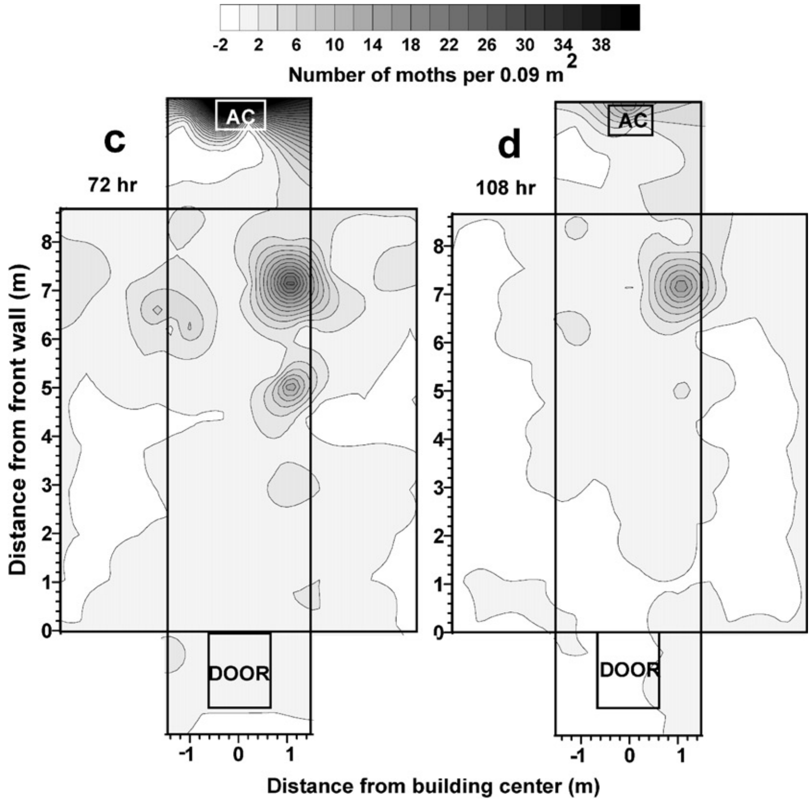

Fig. 6. (*Continued*)

pallets. These analyses revealed that pallets 3, 6, and 8 and the areas immediately surrounding them, were preferred initially by the moths. Later in the infestation period, the moths gradually left their initial resting sites and the population became redistributed between the pallets and the walls. We observed that female moths moved between pallets during the scotophases with a general, overall movement along the return air side of the warehouse towards the AC end (Fig. 6b). In contrast, the males, which had been resting on the walls, began to move to the air inlet filter on the AC during the second photophase. This movement reached a peak at about 84 h after which the males began to die. During this same period, the females (and a few males) were congregated largely on and in the vicinity of pallet 7 (Fig. 6c). The females remained congregated on and around pallet 7 until they died (Fig. 6d).

3.7. Longevity

The number of living moths in the warehouse had begun to decline by 72 h (Fig. 7). Female mortality appeared to occur at a faster rate than that of males. Less than 20% of the initial population survived to144 h and most of these were males. This agrees with the findings

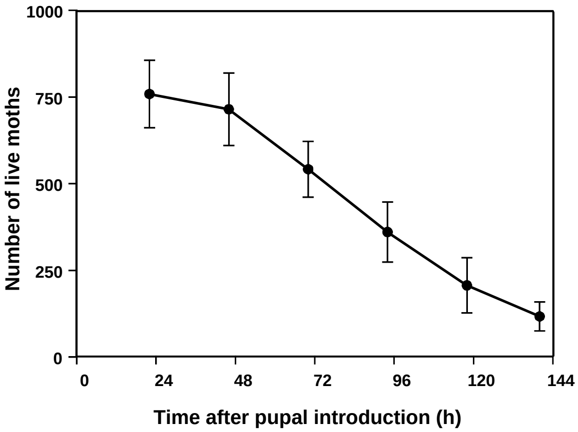

Fig. 7. The total number of live moths observed at various intervals during a typical warehouse test. Each point is the average of four determinations ± SEM.

of Shaaya et al. (1991), who reported that the life span of mated females was about 5–6 d, which was about one-half the life span of unmated females.

4. Summary

Indian meal moth behavior in a warehouse is carefully orchestrated by the photoperiod. It first comes into play by synchronizing the emergence of moths so that they are fully mobile with the onset of a scotophase. Spatial analysis reveals that the females are most active during the scotophases in seeking suitable sites for oviposition. On the other hand, the males are most active during the photophases when seeking receptive females, first by using a flutter dance across the resting surfaces when many females are calling and later, by flying upwind when only a few females are calling. In a closed warehouse, mating is quickly achieved. However, egg laying directly on the commodity was lower than expected, probably because commodity odors may have dissipated over time or may have appeared omnidirectional in a closed warehouse with circulating air, precluding moth orientation to the commodity for oviposition.

Air currents appeared to be a major steering factor in the movement of moths in a closed warehouse with circulating air. Males were observed to aggregate on the AC when the number of "calling" females and putative pheromone levels in the warehouse had declined. Females generally moved in the same direction as males, but at floor level amongst the commodity pallets; even though their movement was between pallets on the return air side of the warehouse, it is not clear whether or not this is a response to air currents. These movements of the moth population within a warehouse were visualized by the sequential plotting of moth distributions over time by the application of spatial analysis. The analytical methods used in this study should have application in other studies investigating the behavior and movement of insect populations.

Appendix

Mean number of moths located on each of the four-monitored warehouse areas designated in Fig. 5. Each point is the average of four determinations ± the standard error of the mean (SEM), except where only two determinations were made (92–108 h).

Time (h)	Wall		Floor		AC inlet		Pallet	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	10.3	6.1	4.7	4.7	2.0	1.2	1.5	1.0
8	18.5	15.8	9.4	9.4	1.0	0.6	2.7	0.6
12	26.7	10.8	47.0	31.2	2.0	1.2	6.0	1.5
20	373.3	60.3	239.7	73.7	2.8	0.2	110.8	21.4
24	463.3	45.1	169.2	82.3	3.8	0.2	134.3	15.4
28	389.5	49.7	80.0	32.9	9.0	2.4	61.0	7.4
32	518.5	48.8	89.3	11.8	13.0	3.2	94.5	9.1
36	539.5	60.0	98.7	31.1	13.0	2.9	111.3	11.3
44	467.8	29.2	136.3	25.9	39.8	4.1	103.8	14.6
48	510.0	52.6	164.8	24.7	49.5	5.2	89.3	10.5
52	401.5	40.9	80.0	36.2	50.8	6.0	48.3	11.0
56	467.3	5.9	122.0	24.9	47.5	6.8	71.0	6.7
60	517.5	44.0	112.8	15.3	36.3	5.3	89.0	5.6
68	406.0	23.8	145.8	33.0	68.0	9.4	69.0	6.6
72	350.8	68.3	136.5	23.5	68.3	14.2	44.0	6.8
76	367.0	46.1	84.5	16.5	60.8	10.0	37.5	5.4
80	303.3	50.7	108.3	12.0	48.5	9.7	34.0	5.7
84	338.0	47.4	117.5	23.6	34.3	9.0	53.3	6.2
92[a]	167.0	(36.0)	144.5	(9.5)	32.5	(5.5)	33.5	(2.5)
96[a]	199.0	(19.0)	84.6	(9.4)	35.5	(8.5)	23.0	(0.5)
100[a]	175.5	(4.5)	84.2	(27.8)	29.5	(5.5)	17.0	(2.0)
104[a]	172.0	(8.0)	103.2	(46.8)	23.5	(2.5)	23.5	(4.5)
108[a]	147.0	(8.0)	75.2	(18.8)	15.5	(1.5)	24.5	(4.5)

[a] Average of two determinations ± (one-half range).

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